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Female-biased incubation and strong diel sex-roles in the Two-banded Plover *Charadrius falklandicus*

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Abstract

The relative contributions of males and females to incubation, and the diel schedules by which incubation is shared, are important breeding system traits. We used infra-red sensitive cameras to record incubation patterns at 13 nests of the Two-banded Plover *Charadrius falklandicus* in the Falkland Islands during both day and night. Because predation risk can affect incubation behaviour, we also recorded the diel pattern of nest predation in the wider study population. We found high nest attendance, female-biased incubation, and strong diel sex-roles, with females incubating during the day and males at night. We also found that incubation intermissions tended to be short but frequent, and were correlated strongly with the diel pattern of nest predations which occurred exclusively in the daylight hours (probably due to the absence of terrestrial mammals from the study site). Our results suggest that sex-roles are unusually strict in the Two-banded Plover, and that these strict sex-roles lead to inequality in incubation sharing and the level of exposure to sources of energetic cost such as disturbance by nest predators.

Keywords

Incubation, Nest camera, Nest Predation, Nocturnal, Sex-role, Temperature data-logger

Introduction

Shorebirds (sandpipers, plovers and allies) exhibit a wide spectrum of sex-roles in incubation, with some species showing uniparental (female-only or male-only) incubation and a majority of species in which the male and female always contribute (Reynolds and Székely 1997). It is increasingly realised that incubation is a highly demanding component of parental care, being both energetically expensive and risky (Amat and Masero 2004; Reid et al. 2002). It is thus a prime candidate for sexual conflict, the divergent interests of males and females over reproduction (Chapman et al. 2003): by transferring the burden of incubation to its partner, an individual could increase the time and energy available for breeding attempts with other partners and potentially increase its fitness (Brunton 1988; Kosztolányi et al. 2009). Variation in the relative contributions of males and females to incubation can thus be a sensitive indicator of sexual conflict and an important trait with respect to natural and sexual selection – as Trivers (1972) noted, heritable variations in parental investment can have major evolutionary consequences. However, the relative contributions of males and females have only been recorded in a small proportion of biparentally incubating bird species (Wallander 2003; Whittingham and Dunn 2001).

Studies of parental care in wild populations often seek to investigate patterns including the relative contributions of males and females to care based on data collected exclusively in the daylight hours (e.g. Bergstrom 1986). While the approach may be acceptable for mainly diurnal behaviours such as the provisioning of young by diurnal altricial birds, it can lead to biased estimates of parental roles whenever the sexes have a tendency to divide care according to a diel schedule. Methods which account for parental activity during both the day and the night are therefore preferable: such methods include the use of infra-red cameras (Thibault and McNeil 1995) passive transponders (Kosztolányi and Székely 2002) and triangulation of radio transmitters (Warnock and Oring 1996).

We present nest-camera data on diel patterns in incubation in the Two-banded Plover *Charadrius falklandicus*, a small biparentally-incubating shorebird (body mass 70 g) that is widely distributed in the southern Neotropical region (del Hoyo et al. 1996). We investigated this species in the Falkland Islands, where it is abundant (Woods and Woods 1997). We quantify the relative contributions of males and

females to incubation, determine whether incubation is shared according to a diel schedule, and explore patterns in nest attentiveness over the course of the day. Because nest predation risk has the potential to explain much of the variation in incubation patterns (Ghalambor and Martin 2002) we also recorded the diel distribution of nest predations in the wider study population using temperature data-loggers (Hartman and Oring 2006).

Methods

Fieldwork

Field data were collected between October and December 2008 on Sea Lion Island at the south of the Falkland Islands archipelago in the South Atlantic (52° 26' 0" S, 59° 5' 0" W); the island has an area of 905 ha, and lacks mammalian nest predators such as cats, foxes and rats. Two-banded Plover nests were located by searching suitable habitat on foot within the study area. Motion-sensitive cameras were then used to monitor incubation routines at 13 nests at which at least one parent had been captured, sexed and colour-ringed, allowing the sexes to be distinguished. Two-banded Plovers can be reliably sexed in the field, as males typically have stronger black breast-bands and a rich chestnut plumage on the nape (Woods 1988). The camera systems are composed of an Infra-Red LED array and Infra-Red sensitive digital camera mounted on a short pole, and a data-logger and power supply which were buried up to 4 m from the nest scrape (Bolton et al. 2007). A software trigger was used to record a series of images whenever movement occurred in the centre of the camera's frame (ie, whenever the sitting bird moved its head, shifted position on the eggs, or left or arrived at the nest). An average of 1381 images were taken per hour of recording. The images were written to SD-type data cards with a unique electronic time stamp. The data cards were changed approximately every 10 hours (mean \pm SD: 10.3 \pm 1.8 hrs, n = 13 nests).

In the nest-camera images, individuals were identified by recording the presence or absence of colour rings on both the outgoing and incoming bird. Additionally, differences between individual males and females in the width and completeness of the upper breast-band allowed identifications to be confirmed while the birds were incubating.

Temperature data-loggers were installed at 50 further nests using methods described by Hartman and Oring (2006) to record the diel timing of predation events. Briefly, a temperature data-logger was buried in the centre of each nest-scape, under approximately 5 mm of lining material; a control data-logger was similarly buried approximately 30 cm from the nest scrape. Of the 50 nests, 27 predation events were recorded and the time of predation was clearly discernable (from a rapid decrease to ambient temperature) in 24 of these.

Data analysis

To compare the relative contributions of males and females over the full day using nest-camera images, 24 on-the-hour images – one for each hour, from 00:00 h to 23:00 h – were taken from each nest, recording the presence of ‘male’, ‘female’ or ‘neither’. Because some records on a given day were often missing (for example, due to a lack of camera memory) or potentially compromised (for example, due to an observer visit to the nest during the proceeding hour) the 24 on-the-hour records were sampled randomly from the remaining ‘good’ records across all recorded days for that nest. If a nest lacked a record for a particular hour on every day of recording, the nest was excluded from this analysis (leaving $n = 8$ nests in total). For each nest, the number of records (of 24) contributed by the male and female were then expressed as a proportion; male and female per-day contributions were compared by subtracting male from female proportions, and testing for a difference from zero (paired t -test). Nests which provided fewer than 24 on-the-hour records were *not* excluded from graph of diel sex-roles because the graph shows the pattern of nest attendance in the population, and not within individual nests.

A ‘shift’ was considered as the period from the time a parent settled on the eggs to the time it left to be replaced by its partner. Change-over times (when one partner replaced the other) were also recorded. Because birds often took breaks (henceforth ‘intermissions’) from incubation during their shift, incubation was broken up into shorter periods (henceforth ‘bouts’). For each nest, the median durations of bouts and intermissions were recorded separately for males and females. Shifts, bouts and intermissions were excluded from analysis if they were compromised by observer activity (for example, the bouts preceding and following observer visits to the nest were excluded).

Rates of intermission in incubation were estimated by counting the number of intermissions (excluding observer-caused intermissions and change-overs between the sexes) that occurred in each two-hour period during the day. Linear quadratic regressions were used to test the relationships between time-of-day and predation events, and time-of-day and frequency of intermissions in incubation; for this test, a single (mean) frequency of intermission was calculated for each time period. Finally, we tested for correlation between the response variables (nest predation events and mean frequency of intermission).

Data are presented as mean values \pm 1 Standard Deviation when normally distributed, and differences between males and females were analysed using paired *t*-tests. Intermission and bout durations and change-over times were not normally distributed and are thus presented as median values with inter-quartile range (1st to 3rd quartile, in parentheses), and analysed using Mann-Whitney *U*-tests. To avoid pseudoreplication, when more than one datum was recorded for a given individual, nest or time-period, an average was calculated for analysis.

Results

Diel patterns of incubation

Incubation was biparental, with males tending to incubate at night and females tending to incubate during the day, and change-overs between the sexes occurring around sunrise and sunset (Fig. 1); female shifts started at a median of 69.0 minutes after sunrise (1.4 – 119.0 min, *n* = 12 nest medians), and male shifts started at a median of 15.0 minutes before sunset (64.4 – -2.5 min, *n* = 13 nest medians).

Including only those nests for which attendance was recorded at least once for every hour of the day (*n* = 8), total nest attendance was 92%, and males were on the nest for a significantly lower proportion of records than females both over a full 24 hours and during the daylight hours only, although they attended the nest on the majority (85%) of the hours of darkness (Table 1).

Consistent with the period of daylight exceeding the dark period, female incubation shifts were significantly longer than those of males, although there was no significant difference between the sexes in the duration of intermissions or bouts of incubation (Table 2).

Change-overs between the sexes were quick, lasting a median of 0.1 minutes (0.1 – 0.2 min, $n = 5$ nest medians). Observer-caused intermissions were relatively infrequent, occurring only when data cards were exchanged (2 – 3 per day). The parents returned quickly to the nest following these visits: from the moment the observer walked away from the nest to the return of the incubating parent took a median 1.7 minutes (1.0 – 3.4 min, $n = 13$ nest medians).

‘Natural’ intermissions in incubation were frequent and varied over the course of the day, with a low rate of intermission at night increasing to a peak rate of intermission during the middle of the day (Fig 2): time-of-day was thus a powerful predictor of intermission rate ($F_{2,9} = 19.69$, $P = 0.001$, $r^2 = 0.81$, $n = 12$ (mean intermission rates)).

Diel pattern of nest predation

We recorded the exact times of 24 nest predation events in our study population; these events followed a diurnal pattern, with no events occurring during the hours of darkness and a peak during daylight hours (Fig 2); thus time-of-day accounted for most of the variation in nest predation frequency ($F_{2,9} = 10.23$, $P = 0.005$, $r^2 = 0.70$, $n = 12$). Intermission rate and nest predation frequency followed the same diel pattern, and were thus highly correlated (Pearson correlation, $r^2 = 0.68$, $P = 0.014$, $n = 12$).

Discussion

The diel sex-roles in incubation are apparently stronger in the Two-banded Plover than in most other *Charadrius* species (Wallander 2003) with males attending the nest for almost all of the night, and females for almost all of the day (Table 1; Fig. 1). The pattern of female incubation during the day and male incubation at night is consistent with other members of the genus (Wallander 2003), although the sympatric Rufous-chested Dotterel *Charadrius modestus* shows a reversal of this pattern (St Clair et al. 2010). A comparison among the biparentally incubating shorebirds demonstrates that the tendency for male incubation at night and female incubation during the day is not a rule: for example, the tundra plovers (*Pluvialis spp*) and several lapwings (*Vanellus spp*) exhibit more female incubation during the night (Byrkjedal and Thomson 1998; Ward 1990). These patterns suggest that among closely related species the same diel

sex-roles tend to prevail, indicating that the roles are often evolutionarily conserved. The other striking pattern is that diel sex-roles in incubation are apparently the norm, with weak or nonexistent diel sex-roles in biparental incubation seldom reported - weak diel sex-roles were reported for three sandpipers (*Calidris spp*) by Norton (1972) and Pierce (1997) although their high-latitude study sites were in perpetual daylight.

Most explanations for diel sex-roles in incubation assume that incubation at different times of day has divergent costs and benefits that males and females are differently equipped to cope with. For example, the daylight-incubating sex may face greater risk from visual predators and be required to sit for more time (as daylight hours exceed night-time hours), whereas the night-time incubating sex must cope with a greater risk from olfactory predators, and possibly a higher energetic cost per unit of time (due to lower temperatures). Added to these factors, temporal variations in prey abundance and feeding opportunities may drastically change the costs of incubation during the day or night, as one sex is constrained to incubate while the other can feed freely. The relative magnitudes of these different costs and benefits, and their differential effects on male, female and offspring fitness, are still largely addressed speculatively rather than empirically.

We found that females experience higher rates of intermission in incubation than males, an effect that appears to be associated with time-of-day rather than sex-specific behaviour because male intermission rate increases through the course of the morning and decreases during the evening (Fig 2). Our results also highlight a candidate mechanism for this difference in intermission rate: a strong diel pattern in nest predation risk which is highly correlated with frequency of incubation intermissions through the day. Because many factors besides predation risk vary according to diel patterns, it is not possible to distinguish causes from consequences in this case – for example, it may be that higher daytime temperatures allow females to leave the nest to feed, while the costs of doing so at night are prohibitive due to lower ambient temperatures. However, it seems probable that the frequent very short intermissions during the day are at least partly the result of anti-predator behaviour (flushing) in response to avian predators such as Striated Caracaras *Phalcoboenus australis*, which are abundant on Sea Lion Island (Woods and Woods 1997). There

are likely to be costs associated with such frequent anti-predator behaviour, including increased energy expenditure (Biebach 1986) and chronically elevated levels of stress hormones such as corticosteroids (Clinchy et al. 2004); the lack of nocturnal nest predators (mammals) at our study site means that these potential costs are faced largely by the female. Furthermore, frequent intermissions are also likely to be costly to the developing embryo, potentially resulting in egg temperature fluctuations away from the developmental optimum, lower mean egg temperatures and consequently long incubation times (Martin et al. 2007; Olson et al. 2006). Consistent with the latter idea, Two-banded Plovers exhibits a remarkably long incubation period of 29.6 days (St Clair et al. in prep.).

Once specialised diel sex-roles in incubation arise, there are intriguing potential consequences for the evolution of breeding systems. For example, in biparental species the adaptation of the sexes to particular incubation roles may be reinforced by positive feedback: adaptation promotes role specialisation and role specialisation favours adaptation. The resulting reinforced specialisation of sex-roles may strongly favour continued cooperation and biparental care (Barta et al. in prep), as specialised parents may experience higher fitness than unspecialised ‘jack-of-all-trades’ parents through improved survival of themselves and their offspring. In turn, their specialisation may mean that they are unable to effectively assume the role of the other parent, ensuring that desertion by one parent severely reduces the success probability of the reproductive attempt. Such feedback adds a further dimension to the complexity of breeding system evolution, and it is increasingly realised that mate choice, mating systems and parental care are strongly interrelated (Alonzo 2009; Székely et al. 2000). If specialisation in parental roles reaches a threshold level, it could represent a powerful selection pressure for social monogamy, and a mechanism for the contingent irreversibility (*sensu* Szathmáry and Maynard Smith 1995) of biparental cooperation.

A further possibility is that if diel sex-roles are ‘hard-wired’ in that change-over behaviours are triggered by changing light levels at dawn and dusk, latitudinal shifts in breeding range towards the poles (where hours of darkness are reduced) would lead to changes in the relative amounts of incubation contributed by males and females; this idea may be assessed in the Two-banded Plover by testing the prediction

that incubation will be more evenly shared at lower latitudes in continental South America where there is greater parity between the hours of daylight and darkness. While biparental care may be most evolutionarily stable when day and night are not of very different lengths, changes in day-length would effectively reduce the time and energy available to partners of one sex for extra-pair courtship or polygamy, while increasing the variance in extra-pair possibilities for the other. In consequence, among taxa with an evolutionary history of strict diel sex-roles we might expect a higher incidence of uniparental care at very high latitudes, a trend which has been shown to exist among shorebirds in general with respect to post-hatching care (Garcia-Peña et al. 2009) but which has not yet been addressed with respect to care during incubation.

In summary, our findings show that Two-banded Plover pairs share incubation according to a diel schedule, and that males tend to incubate at night and females during the day. This diel schedule is associated with unequal sharing of incubation over 24 hours (because day-length exceeds night-length, females spend more time at the nest) and with other inequalities, such as a higher rate of intermissions in incubation for females. The diel pattern of intermissions is consistent with frequent flushing during the day in response to elevated predation risk, although there are other possible causes such as the need to forage or express territorial behaviour. These patterns suggest several directions for future research, both into the proximate causes of variation in incubation behaviour (factors such as photoperiod and predation risk), and the potential interaction between sex-role specialisation and the evolution of breeding systems.

Zusammenfassung

Die vornehmlich weibliche Bebrütung und stark tageszeitabhängigen Geschlechterrollen des Falklandregenpfeiffers *Charadrius falklandicus*

Die relative Beiträge von Männchen und Weibchen zur Bebrütung und der tägliche Rhythmus, in dem die Bebrütungswechsel erfolgen, sind wichtige Merkmale von Fortpflanzungsstrategien. An Hand von Infrarotkameras wurden Bebrütungswechsel an 13 Nestern des Falklandregenpfeiffers *Charadrius falklandicus* auf den Falklandinseln bei Tag und Nacht aufgezeichnet. Weil Bedrohung durch Fressfeinde

das Bebrütungsverhalten verändern kann, wurden außerdem tägliche Erscheinungsmuster von Nesträubern in der gesamten Studienpopulation erfasst. Wir beobachteten hohe Nestpräsenz, Bebrütung vermehrt durch das Weibchen und ausgeprägte, tageszeitabhängige Geschlechterrollen, wobei Weibchen tagsüber brüteten und Männchen nachts. Wir fanden eine starke Korrelation zwischen Bebrütungsaussetzern, die meist kurz waren, aber häufig vorkamen, und dem Auftreten von Nesträubern, die nur tagsüber erschienen (wahrscheinlich, weil am Studienort keine terrestrischen Säugetiere vorkamen). Unsere Ergebnisse legen nahe, dass Geschlechterrollen bei Falklandregenpfeifern ungewöhnlich genau festgelegt sind und dass diese strengen Geschlechterrollen zu einer Ungleichheit führen, sowohl in der Aufteilung der Bebrütung als auch in der Belastung durch Ereignisse mit hohen energetischen Kosten, wie die Beeinträchtigung durch Fressfeinde.

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Figures & Tables

Table 1: Incubation sharing by Two-banded Plover pairs in the Falkland Islands.

Proportion of on-the-hour records for which nests was attended by the male, female or no bird, for full days (24 h), daytime only (05:00 to 20:00 inclusive) and night-time only (21:00 to 04:00 inclusive).

	Proportion of records (mean \pm SD)			Sex comparison (paired <i>t</i> -tests)		
	Male	Female	Neither	<i>n</i> nests	<i>t</i>	<i>P</i>
Full day	0.34 \pm 0.08	0.58 \pm 0.06	0.08 \pm 0.04	8	4.83	0.002
Daytime only	0.06 \pm 0.08	0.85 \pm 0.09	0.09 \pm 0.07	8	14.60	<0.001
Night-time only	0.85 \pm 0.14	0.05 \pm 0.07	0.09 \pm 0.13	8	12.38	<0.001

Table 2: average durations of incubation shifts, bouts and intermissions in the Two-banded Plover. Shifts were normally distributed (mean \pm 1 SD.; paired *t*-test). Bout and Intermission data were left-skewed and treated nonparametrically (median, interquartile range; Mann-Whitney U-test).

	Duration \pm SD or (q1 – q3)		Sex comparison	
	Male	Female	<i>t</i> or <i>U</i> (<i>n</i> pairs)	<i>P</i>
Shifts (hrs)	8.7 \pm 1.7	15.0 \pm 1.2	<i>t</i> = 7.92 (8)	< 0.001
Bouts (mins)	19.5 (8.8 – 30.5)	10.5 (8.1 – 15.2)	<i>U</i> = 208 (13)	= 0.108
Intermissions (mins)	1.0 (0.7 – 2.2)	1.3 (0.6 – 1.6)	<i>U</i> = 158 (13)	= 0.383

Figure legends

Figure 1: Diel sex-roles in nest attendance in the Two-banded Plover in the Falkland Islands. On-the-hour nest attendance records (male, female or neither) were sampled from nest camera footage of 13 nests (maximum one record per nest per hour) and expressed as a proportion of the total number of records for each hour. Median sunrise occurred at 04:43h and sunset at 20:52h.

Figure 2: Rate of intermission in the Two-banded Plover. Each point represents the number of intermissions at a single nest during a two hour period; jitter is added for clarity. Change-overs and observer-caused intermissions are not counted here. Black symbols for male-only periods, Grey symbols for female-only periods, and Empty symbols for periods during which a change-over occurred (ie both sexes present). Bars show frequency of actual nest predations recorded by temperature data-loggers over the course of the study, in two-hour bins.

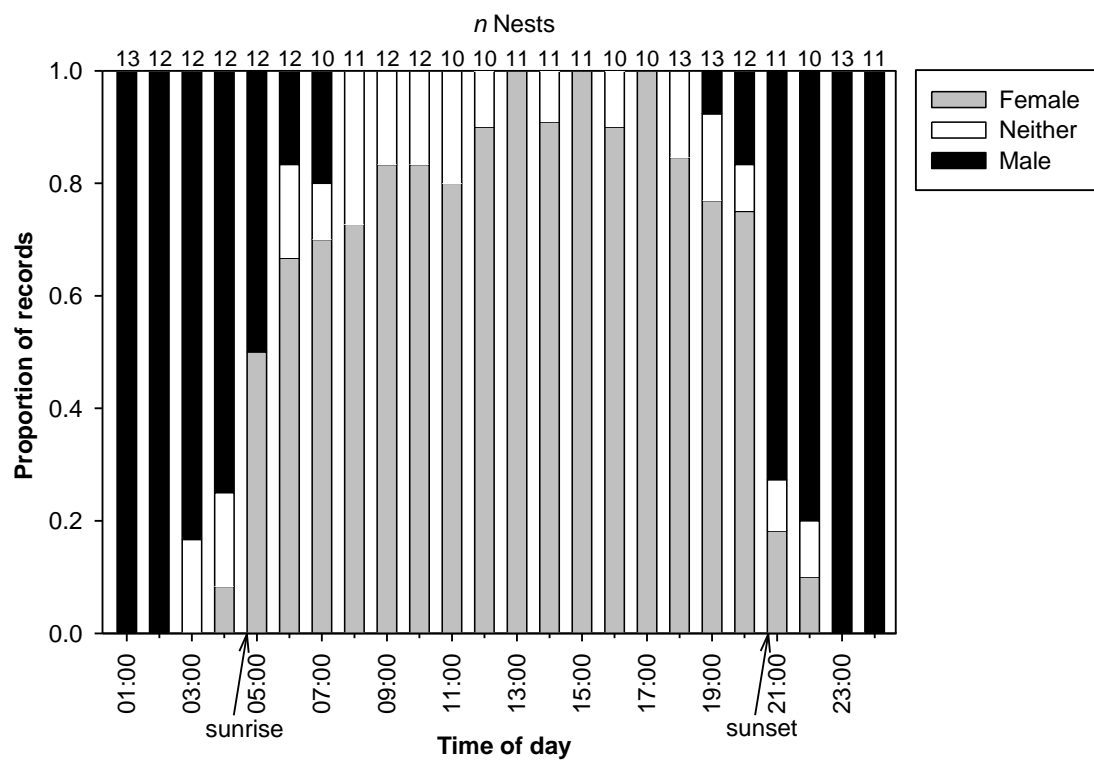
Figure 1

Figure 2

